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Blast disease and wheat production in Brazil

Abstract - This review paper presents the current context of wheat production in Brazil, the management strategies to reduce yield losses due to blast, and the biotechnological approaches to improve wheat resistance. Wheat blast or brusone is caused by the Magnaporthe orvzae Triticum (MoT) pathotype fungus that can infect all the aboveground parts of the plant. The main symptom of the blast disease is spike bleaching that impairs grain production, causing yield losses up to 100% in susceptible wheat cultivars. The first world report of blast in wheat spikes was in Brazil, in 1985, and, currently, the disease is the main constraint to wheat cultivation in tropical and subtropical areas of the Cerrado and Mata Atlântica biomes. For a long time, the use of fungicides has been found to be ineffective under high-pressure disease conditions. However, recent works have pointed out that fungicide efficiency depends on the integration of other control measures, particularly the choice of cultivars with moderate resistance. In this review paper, the high variability of wheat reaction to MoT is presented, as well as a panel of resistant or moderately resistant cultivars (including non-2NS carriers), promptly available for cultivation in regions where blast is endemic.

Index terms: *Magnaporthe oryzae*, *Triticum aestivum*, brusone, chemical control, genetic resistance, management.

Brusone e produção de trigo no Brasil

Resumo – Esta revisão apresenta o contexto atual da produção de trigo no Brasil, as estratégias de manejo para reduzir perdas de rendimento de grãos devido à brusone e as abordagens biotecnológicas para melhorar a resistência do trigo. A brusone do trigo é causada pelo fungo Magnaporthe oryzae patótipo Triticum (MoT) que pode infectar toda a parte aérea da planta. O principal sintoma da doença é o branqueamento das espigas que prejudica a produção de grãos, com perdas que podem chegar a 100% em cultivares suscetíveis. O primeiro relato mundial de brusone em espigas de trigo foi feito no Brasil, em 1985, e a doença atualmente é a principal restrição ao cultivo de trigo nas áreas tropicais e subtropicais dos biomas Cerrado e Mata Atlântica. Por muito tempo, o uso de fungicidas foi considerado ineficaz sob condições de alta pressão de doença. No entanto, trabalhos recentes apontam que a eficácia dos fungicidas depende da integração de outras medidas de controle, principalmente da escolha de cultivares com resistência moderada. Neste artigo de revisão, apresentam-se a alta variabilidade de reação do trigo ao MoT, bem como um painel de cultivares resistentes ou moderadamente resistentes (incluindo não portadoras da translocação 2NS), prontamente disponíveis para cultivo em regiões onde a brusone é endêmica.

Termos para indexação: *Magnaporthe oryzae, Triticum aestivum*, brusone, controle químico, resistência genética, manejo.

Introduction

The first world occurrence of blast disease in wheat spikes was reported in Brazil, in the state of Paraná, in 1985 (Igarashi et al., 1986). The disease is caused by Magnaporthe oryzae B.C. Couch 2002, a fungus that can infect different parts of the plant but causes most damage to the spikes (Prestes et al., 2007). Sap translocation during grain filling is interrupted when the pathogen infects the rachis, leading to diseased spikes, which present discoloration or bleaching and small and wrinkled grains, whose use is impaired (Goulart, 2007).

Over the years, the pathogen was disseminated to different wheat-producing regions in Brazil, from the Southern to the Midwestern regions of the country, particularly to the states of Mato Grosso do Sul, Rio Grande do Sul, São Paulo, Goiás, and Minas Gerais, as well to the Cerrado region in the Midwest (Goulart et al., 2007). Besides in Brazil, the disease was also reported in tropical areas of neighboring South American countries, such as: Paraguay, in 1987; Bolivia, in 1996; and Argentina, in 2007 (Kohli et al., 2011).

For more than 30 years, wheat blast was restricted to South America; however, there is a risk of the disease spreading to countries with climatic conditions similar to those of the subtropical and tropical areas of Brazil (Duveiller et al., 2016). In 2016, the disease was identified in Bangladesh in South Asia, where wheat fields had to be burned to contain the pathogen (Islam et al., 2016), so that it would not spread to neighboring major wheat-producing countries. In 2017, the first citation on the occurrence of wheat blast in India, the second world wheat producer with the longest frontier with Bangladesh, was made (Bhattacharya & Pal, 2017). Shortly after, during the 2017–2018 rainy season, wheat blast symptoms were also observed in Zambia in Africa (Tembo et al., 2020). This recent and fast pathogen dissemination from Asia to Africa poses a threat to the food security of many countries reliant on wheat as their staple food.

Despite this worldwide spread of the disease, the most significant volume of studies was developed in Brazil from the disease's first description until mid-2010 when different foreign institutions began carrying out researches on the subject (Duveiller et al., 2016). Comparing the decade of 2012–2021 with the previous one, there was a twofold increase in the number of publications on topics related to wheat blast and its pathogen (Figure 1). Moreover, the designation "wheat blast" has become increasingly common in publications - before 2015, the name Magnaporthe oyzae Triticum pathotype was rarely used. Despite this growing knowledge, the situation concerning blast disease in Brazil is unique because there it is not a threat but already endemic. The pathogen is currently present in the tropical and subtropical fringes of wheat-producing regions, showing how the epidemic occurrence of the disease is strictly dependent on environmental conditions. High temperatures and humidity during the wheat-heading stage, for example, favor outbreaks (Fernandes et al., 2017). For this reason, the highest intensity of symptoms occurs in crops in the north and northwest of the state of Paraná, Brazil, and in the areas considered nontraditional for wheat production where control measures are a primary issue.

This review paper presents the current context of wheat production in Brazil, the control measures that can be adopted – mainly genetic control –, and the application of biotechnological strategies to potentially improve wheat resistance.

Wheat production in Brazil

Wheat (*Triticum* spp.) is the second most produced cereal in the world and accounts for 19% of the daily calories and 21% of the protein requirements in human



Figure 1. Number of publications per year retrieved from the Web of Science database on September 6, 2021, using the terms wheat AND (pyricularia OR magnaporthe) in the title, abstract, author's keywords, and Keywords Plus of the publication.

diets (Tadesse et al., 2019). It is cultivated worldwide and can provide up to 80% of energy in developing countries (Schnurbusch, 2019). In 2019/2020, wheat production was 763 million tons (FAO, 2020), coming after corn (*Zea mays* L.) production, with 1.1 billion tons (Amis, 2020). Although 5.15 million tons were produced in Brazil, 7.2 million tons had to be imported to meet the internal demand of 12 million tons (Amis, 2020). In this unfavorable context for domestic consumption, Brazilian production is still far from the country's potential for wheat cultivation.

Triticum aestivum L. is a hexaploid species called "common" or "bread" wheat, covering more than 95% of the world's wheat production, while Triticum durum var. durum is a tetraploid species, referred to as "pasta wheat" or "durum wheat" for pasta production, being adapted to hot and dry conditions of cultivation (Sharma et al., 2020). In Brazil, common wheat is the only species grown and as a spring crop. Worldwide, spring wheat cultivars account for 65% of the total bread wheat production (Tadesse et al., 2019). The presence or absence of genes controlling the need of vernalization defines winter and spring wheats, respectively (Crofts, 1989). A minimum period with lower temperatures between 0 and 5°C is required for the heading of winter wheats, but not for spring wheats (Royo et al., 2020).

The wheat area production in Brazil is historically subdivided into three regions: the South, including the states of Rio Grande do Sul, Santa Catarina, and the south of Paraná; the Southeast-Midwest, covering the states of Paraná, Mato Grosso do Sul, and São Paulo; and the Midwest, including the states of Goiás, Minas Gerais, Mato Grosso, and Bahia, as well as Distrito Federal (Reunião..., 2018). However, four homogeneous regions of adaptation of wheat cultivars (RHACT) are determined based on pluviosity, temperature, altitude, and historical data of grain yield (Figure 2) (Cunha et al., 2006). Value for cultivation and use tests are conducted in these regions (Cunha et al., 2011). The humid region, from Rio Grande do Sul to the north of Paraná, is subdivided from cold to hot regions (Regions 1 and 2). Region 1 is cold, whereas Region 2 is hot and the main wheat-producing area in the country. Region 3, considered moderately dry and hot, includes the north of Paraná, south of São Paulo, and part of Mato Grosso do Sul, where it is possible to produce rainfed wheat, while region 4, which is hot and dry, encompasses parts of São Paulo and Mato Grosso do Sul, besides Goiás, Distrito Federal, Minas Gerais, Mato Grosso, and Bahia (Cunha et al., 2011). RHACT 4 has a typical tropical climate and is currently considered a nontraditional area for wheat production in Brazil. The Midwestern region of the country, characterized by the Cerrado biome, is the current agricultural frontier for the expansion of wheat cultivation (Pasinato et al., 2018).

In Brazil, wheat is cultivated in regions with temperate, tropical, and subtropical climates (Cunha et al., 2011), covering an area of 2.04 million hectares in 2019 (Conab, 2020). The states of Rio Grande do Sul and Paraná accounted for 80% of the national wheat production (Conab, 2020). In 2019, 150 thousand hectares were cultivated with wheat in the Midwestern region, where the crop is grown both in irrigated (between May and September, with favorable temperature conditions) and rainfed systems, being exposed to thermal and water stresses, with sowing dates from March to April. Compared with the mean national yield of 2.5 Mg ha-1, wheat yield is higher under irrigation, reaching 5.0 to 7.0 Mg ha⁻¹, and lower in rainfed conditions (Albrecht et al., 2007). It should be noted that, even if limited to high altitudes, the potential area of the Cerrado region is 2 to 3 million hectares (Albrecht et al., 2007).

Besides its potential area, the Cerrado region provides a competitive advantage for wheat production. Where a tropical climate prevails, wheat can be cultivated in the off-season of summer crops, enabling harvest in the absence of rain, which ensures the obtention of a high-quality product (Albrecht et al., 2007). During this period, wheat has not yet been harvested in the traditional cultivation areas in the South of the country and in Argentina, which is the leading wheat exporter to Brazil. However, there are constraints to growing rainfed wheat, which is sown in early February, right after soybean (Glycine max L.) harvest, mainly the occurrence of blast or brusone. Blast disease is endemic in regions with a predominantly hot and humid climate, as well as in the north and northwest of Paraná and in the Brazilian Cerrado, where major outbreaks have been reported (Torres et al., 2009; Embrapa Trigo, 2019).

Particularly in the Cerrado region, where the potential area for wheat cultivation is superior to 2 million hectares, dealing with blast disease is essential



Figure 2. Homogeneous regions of adaptation of wheat (*Triticum aestivum*) cultivars in Brazil. Brazilian states and federal district: BA, Bahia; DF, Distrito Federal; ES, Espírito Santo; GO, Goiás; MG, Minas Gerais; MS, Mato Grosso do Sul; MT, Mato Grosso; PR, Paraná; RJ, Rio de Janeiro; RS, Rio Grande do Sul; SC, Santa Catarina; SP, São Paulo; and TO, Tocantins. Source: adapted from Cunha et al. (2011).

for Brazil to achieve self-sufficiency. Historically, wheat production in the country only supplies 50% of domestic consumption. In the following topic, the characteristics of the disease and state of the art on control strategies are presented.

Blast disease

For hundreds of years, blast disease has been known in rice (*Oryza sativa* L.), being the main disease of this crop, reducing yields by 10–35% annually (Li et al., 2019). So much so that *Magnaporthe oryzae* x rice pathosystem has become a model for host-pathogen interactions. *Magnaporthe oryzae* B.C. Couch and L.M. Kohn (anamorphic synonym *Pyricularia oryzae* Cavara) was considered, by the international community of plant pathologists, as the most scientifically/economically important fungal plant pathogen (Dean et al., 2012). It belongs to a species complex (Zhang et al., 2016), whose subgroups are distinguishable by their mating types, phylogenetic characteristics, and restricted host range.

Among the wheat diseases of economic importance, blast is considered recent, which explains the evident lack of knowledge regarding the disease (Cruz & Valent, 2017). Castroagudín et al. (2016), for example, investigated whether Oryza and Triticum pathotypes were distinct at species level. Using ten housekeeping loci for the analyses of 128 isolates, the authors concluded that isolates from wheat and other Poaceae hosts grouped into a separate clade were a new species, called Pyricularia graminis-tritici, which causes wheat blast. Subsequently, the species status of the wheatinfecting population of the fungus was reassessed using whole-genome sequence information for 76 M. oryzae isolates sampled from 12 genera of hosts (Gladieux et al., 2018). It was evidenced that M. oryzae is subdivided into multiple lineages, preferentially associated with one host plant genus (Gladieux et al., 2018). Moreover, researchers from different groups reached a consensus that distinct *M. oryzae* lineages, sharing a high degree of genome sequence similarity, are responsible for each severe blast disease (Valent et al., 2019). The obtained results are indicative that P. graminis-tritici should not be used as the species name for the wheat blast pathogen, which should be referred to as Magnaporthe oryzae Triticum (MoT) pathotype.

The MoT pathotype can infect wheat in all stages of plant development. Seeds, when infected, can be asymptomatic, but have a high efficiency in transmitting the pathogen (Reis et al., 1995). Diseased seeds can play an essential role in long-distance dispersal, being a source of primary inoculum in new areas. This hypothesis explains the outbreak in 15,000 hectares in the south of Bangladesh, where the disease was caused by a MoT isolate with a strong genetic identity to a strain from South America (Islam et al., 2016; Ceresini et al., 2018). Depending on the wheat genotype and disease levels, there also may be a lower germination under field conditions (Gomes et al., 2017). However, in seedlings, the appearance of symptoms is reduced, even with high incidences of the pathogen in seeds (Gomes et al., 2007).

In different parts of the wheat plant, the pathogen can produce highly diverse lesions, with different colors and shapes (Figure 3). Different types of lesions can be observed: pinhead-sized spots; small or enlarged brown lesions with no distinguishable center; and typical blast lesions, which are elliptical to elongate, with white to light-brown centers and dark-grey to reddish-brown borders (Torres et al., 2016). The types of lesions can be used to distinguish between resistant and susceptible reactions in rice plants. However, this is not the case for wheat plants, which commonly present a mesothetic reaction, i.e., different types of lesions in the same part of the plant (Torres et al., 2016).

In rice, M. oryzae is typically a foliar pathogen. Symptoms in panicles are observed after foliar infection, but without specialization within the pathogen population regarding the type of organ infected (Ghatak et al., 2013). In wheat, older leaves are more susceptible to the pathogen and thousands of conidia can be produced on basal leaves (Cruz et al., 2015). In field conditions under inoculation, low severities of blast in flag leaves (<0.45%) and low disease progress were observed (Gomes et al., 2019). However, even with a lower severity, the foliar infection of susceptible cultivars can produce secondary inoculum, which facilitates pathogen dissemination from plant to plant, following a polycyclic pattern (Gongora-Canul et al., 2020). However, the epidemiological role of an initial leaf infection on disease progress is still poorly understood for wheat cultivars with different levels of genetic resistance.

MoT infects all the aboveground parts of the wheat plant, but the typical and most destructive symptom is the partial or total discoloration of spikes (Figure 4). Under field conditions, bleaching symptoms are highly noticeable because the spikes show a coloration similar to that at physiological maturity, while all other vegetative parts are still green. In this case, spike fertility may be partially or fully compromised, depending on when the infection occurs (Goulart et al., 2007). Spike infection causes direct damages to wheat grain yield, since sap translocation during grain filling is interrupted due to plant tissue colonization by the pathogen (Goulart et al., 2007). This results in grains that are poorly developed, small, wrinkled, and with a low specific weight (Ferreira et al., 2020). Losses can range from low levels to almost 100% (Kohli et al., 2011). During five years/periods of evaluation in the state of Mato Grosso do Sul, the mean reduction in grain yield was of 32% (Goulart, 2005), whereas, in 2004, losses were from 10.5 to 13.0% (Goulart et al., 2007); however, the greatest reductions in grain yield



Figure 3. Types 1, 2, 3, and 4 of lesions in leaves and spikes of wheat (*Triticum aestivum*) inoculated with *Magnaporthe oryzae Triticum*. Photos: Gisele Abigail Montan Torres.

did not always occur in the genotypes with the highest blast incidences. Lower losses with comparable disease indices indicate a tolerance reaction to wheat blast (Dianese et al., 2021). However, in other reports, grain yield decreased significantly with increasing disease incidence (Goulart et al., 1996) and severity (Trindade et al., 2006). Considering incidence and severity for the calculation of a disease index, significant correlations with yield losses were reported, ranging from 62.8 to 80.1% (Coelho et al., 2016). Regardless of how the disease is quantified, losses depend on the moment of spike infection – higher losses occur at the grain formation stage – and on the host plant resistance.

Blast symptoms in wheat rachis were recently found to be important for the characterization of genetic resistance (Ferreira et al., 2020). When the pathogen infects the rachis (central spike axis of certain grasses), it causes a necrotic and shiny lesion with irregular borders. This lesion corresponds to the penetration site of the fungus in the plant, commonly called "infection point". It was believed that each infected rachis presented only one infection point and bleaching would start from it; however, a variation in the number of infection points on the rachis (ipr) was observed under inoculation and also under field conditions (Figure 5). In fact, the study by Ferreira et al. (2020) was the first to report the number of ipr as an important feature of wheat phenotyping for resistance to blast disease. Wheat susceptible genotypes present few ipr, while the resistant ones have several of them (Figure 6). Therefore, there is an inverse relationship between the number of ipr and bleaching severity (Ferreira et al., 2020). Furthermore, genetic studies revealed the segregation of ipr data in a population of doubled-haploid wheat lines, reinforcing it as an inheritable trait (Ferreira et al., 2021).

The initial steps of the infection process of *M. oryzae* in wheat are similar to those observed in rice (Cruz et al., 2016b). Since *M. oryzae* has a hemibiotrophic lifestyle, the initial invasions are biotrophic, colonizing living plant cells, followed by the necrotrophic stage that promotes plant cell death (Ribot et al., 2008). After a period of four to five days, the first symptoms appear, necrotic lesions develop, and conidia reproduction occurs. The pathogen can repeatedly sporulate for



Figure 4. Contrast in the development of the spike bleaching symptom in wheat (*Triticum aestivum*) when comparing the susceptible cultivar, BRS 209, and the resistant genotype, CBFusarium ENT014, at nine days post-inoculation. HC, healthy control, without inoculation; C, control treatment, mock-inoculated spike; and I, inoculation treatment, spikes inoculated with *Magnaporthe oryzae Triticum*. Photos: Jéssica Rosset Ferreira.

around 20 days, and each *M. oryzae Triticum* conidium can cause a new blast lesion (Cruz et al., 2015). In inoculated wheat rachises, pathogen sporulation was influenced by both temperature and relative humidity, but not by the interaction of the two factors. Higher and faster sporulation occurred at 28 rather than at 23°C with a relative humidity between 95 and 100% (Alves & Fernandes, 2006). In a study quantifying the



Figure 5. Variability in the number of infection points on the rachises from different wheat (*Triticum aestivum*) genotypes inoculated with *Magnaporthe oryzae Triticum*. Photos: Jéssica Rosset Ferreira.



Figure 6. Contrast in the number of infection points on the rachis of the BRS 209 susceptible cultivar and the CBFusarium ENT014 resistant genotype of wheat (*Triticum aestivum*). C, control treatment, mock-inoculated rachises; and I, inoculation treatment, rachises inoculated with *Magnaporthe oryzae Triticum*. Photos: Jéssica Rosset Ferreira.

sporulation of two isolates of *M. oryzae Triticum* in wheat plant segments under different temperatures, the highest production of conidia was observed between 24 and 27°C, independently of the isolate and plant segment (Kovaleski et al., 2020).

The development of spike bleaching symptoms is influenced by the interaction between temperature and the duration of the spike wetting period. No symptoms were noticed at a spike wetting period smaller than 10 hours, whereas the lowest disease intensity occurred at 15°C and the highest, between 25 and 30°C (Cardoso et al., 2008). Under the conditions of wheat cultivation in the state of Paraná, a weather-based model was developed considering both inoculum potential and favorability for infection (Fernandes et al., 2017). In epidemic years, increased humidity and warm temperatures are decisive for inoculum buildup during the period preceding spike emergence (Fernandes et al., 2017). These environmental blast prone conditions are common in Paraná and in the Cerrado region. Therefore, forecasting of rainy days and warm temperatures during the heading and grainfilling stages is conditio sine qua non for the adoption of preventive chemical control measures.

Strategies for wheat blast disease control

Infected seeds can effectively be the primary source of inoculum of MoT. In wheat seeds, M. oryzae remains viable for periods of up to 22 months (Reis et al., 1995). However, the pathogen's ability to survive and be transmitted by seeds can be minimized by fungicide seed treatment. Many fungicides eradicate M. oryzae from infected wheat seeds (Goulart & Paiva, 1991). In addition, under field conditions, the transmission of the pathogen from seeds to seedlings was not observed when the fungicides with the best results were used (Goulart & Paiva, 1991). Currently, there are five commercial fungicides registered for wheat seed treatment, in order to control M. oryzae (Agrofit, 2020), and their active ingredients are: iprodione, fluazinam + thiophanate-methyl, difenoconazole, difenoconazole mixed with metalaxyl-M and thiamethoxam, and carboxin with thiram.

The occurrence of blast disease on the aboveground parts of wheat plants is strictly dependent on environmental conditions. In the tropical region, sowing must be avoided at the beginning of the period defined in the agricultural climatic risk zoning for the wheat rainfed system, so that favorable conditions for disease development do not occur at the heading phase. Under irrigation, independently of wheat genotypes, blast incidence is significantly lower in sowing dates in May than in March in the state of Minas Gerais (Coelho et al., 2016). To support decision-making on the application of fungicides in the boot stage of the wheat crop, the Sisalert platform should be used, since it provides blast epidemic risk forecasts and alerts, based on a collection of meteorological data and processing of information by epidemiological models (Sisalert, 2020).

Considering that controlling diseases of the aboveground parts of wheat plants is essential to reduce damage to grain yield, the efficiency of three active ingredients was evaluated for blast control. All tested fungicides – epoxiconazole + pyraclostrobin, tebuconazole + trifloxystrobin, and tebuconazole –, caused a reduction in leaf blast severity. However, these fungicides were inefficient in controlling spike blast regardless of plant genotype (Rocha et al., 2014). Despite this, under different conditions of inoculation, Pagani et al. (2014) obtained a 55% control of blast severity in wheat spikes, using the same synthetic fungicides.

Goulart et al. (1996) observed a 20% control of blast incidence in wheat spikes when applying a fungicide at the beginning of the heading stage, a result that was not found by Rocha et al. (2014) when applying fungicides for the second time in the intermediate phase of anthesis. Therefore, the use of two or three fungicide applications has similar results on grain yield, conditioned to the first application at the heading stage (Goulart et al., 1996). Using the same three fungicides as Rocha et al. (2014), but with the first application at early heading and the second one at the milk-growth stage, Pagani et al. (2014) reported a reduction in spike blast severity from 35-72%. In Brazil, the preventive use of fungicides is endorsed because the main damage caused by the disease is associated with its occurrence on wheat spikes. Therefore, the beginning of heading is the recommended phase for the first application of fungicides aiming to control the disease (Reunião..., 2018). Regular fungicide applications can be made every ten days only if conditions remain favorable for the disease (Reunião..., 2018).

Regarding chemical control, its efficiency has been reported to be low in several studies, being related to symptom intensity in wheat spikes (Cruz et al., 2019). Since 2010, a working group was formed to carry out cooperative network trials, to generate information on the efficiency of fungicides in the control of wheat blast; the research results are made available annually (Santana et al., 2019). The scope of chemical control has been presented in analyses of more than 40 field trials (Ascari et al., 2021). Even with the application of the best performing fungicides, the average control efficiency reached 49% for incidences up to 25%, but only 23% for incidences ranging from 75 to 100% (Reunião..., 2018).

Factors related to both the host plant and pathogen also influence the efficiency of fungicides in the control of wheat blast. The shape of the spike, for example, makes uniform coverage difficult, reducing the deposition of products in the rachis, which is the main site of pathogen infection (Goulart et al., 1996; Rocha et al., 2014). Moreover, studies on fungicide application technology are still incipient concerning blast control. However, the use of flat jet nozzles proved to have potential to reduce the severity of the disease in wheat spikes (Boaretto et al., 2017).

For wheat blast control on the aboveground parts of plants, 48 commercial products are currently labeled, including 16 triazoles and 8 mixtures of triazole and strobilurin. At the heading stage, three or more fungicide applications are performed by wheatgrowing producers to control wheat blast (Cruz et al., 2019). This scenario favors a high selection pressure on wheat pathogens, as shown by Castroagudín et al. (2015) and Poloni et al. (2020). These authors found that the resistance of M. oryzae to strobilurin and triazoles is widespread in Brazil, which is why it is recommended to alternate these products with ones that have a low risk of causing resistance. The use of mancozeb, a product multisite and with a low risk of selection of resistant pathogen isolates, was shown to be economically viable with two sprays (Goulart et al., 1996). Formulations containing mancozeb have performed well in cooperative network trials in Brazil (Reunião..., 2018; Cruz et al., 2019), leading to a reduction in grain yield losses depending on the evaluated site.

Therefore, the use of fungicides to control blast on spikes is feasible, even under medium to high blast intensity conditions (Cruz et al., 2019). Under these conditions, fungicide applications have influenced the reduction of both the disease index and yield losses. However, comparative data have shown that, in Brazil, blast intensity is higher and the reduction in grain yield losses with the application of fungicides is lower than in Bolivia, for example (Cruz et al., 2019). These varying results may be due to the different levels of blast resistance of the used cultivars and to the timing of fungicide application (Cruz et al., 2019). Furthermore, previous information about the resistance of wheat genotypes can also impact fungicide efficiency. Rios et al. (2016) reported that, under inoculation conditions, without and with fungicide treatment, susceptible and resistant wheat cultivars showed different performances. The authors found that the combined use of resistant cultivars and fungicide led to a greater reduction in disease progress, as well as a decrease in the number of fungicide applications, when using a resistant cultivar.

Genetic resistance

Associated with fungicide use and management strategies, it is essential to choose wheat cultivars with higher levels of resistance to the causal agent of blast. Therefore, the genetic resistance of the wheat cultivar also impacts the efficiency of the adopted control measures. While more than 100 blast resistance genes (R genes) have been mapped in rice, of which 35 have been cloned (Wang et al., 2017), only nine R genes of resistance to Magnaporthe spp. were identified in wheat: Rmg1, Rmg2, Rmg3, Rmg4, Rmg5, Rmg6, Rmg7, Rmg8, and RmgGR119 (Singh et al., 2021). The wheat R genes specifically effective against MoT are Rmg2, Rmg3, Rmg7, Rmg8, and RmgGR119. Rmg1 (synonymous *Rwt4*) and *Rmg6* (synonymous *Rwt3*) were identified in 94.4 and 72.2% of 36 Brazilian wheat cultivars, respectively (Inoue et al., 2017). Rmg8 is supposed to be the most common R gene in wheat accessions since it was found in 18 resistant genotypes from a group of 520 landraces of common wheat collected in Eurasia, Africa, and the Americas and screened for wheat blast (Wang et al., 2018). However, Rmg8 has not yet been identified in genotypes from South America.

Rmg7, *Rmg8*, and *RmgGR119* confer wheat blast resistance to *Triticum* isolates at the seedling and heading stages (Anh et al., 2015; Tagle et al., 2015; Wang et al., 2018). However, studies with a large

number of genotypes have shown that there is no or little correlation between disease severity in seedling and in adult plant stages (Maciel et al., 2014; Cruppe et al., 2020). These results, supported by the absence of colocalization of quantitative trait loci (QTL) at the seedling and heading stages (Goddard et al., 2020), are indicative that different genes are involved in the resistance mechanisms of wheat to blast disease depending on the plant tissue/organ. Wang et al. (2018) also observed that the *Rmg8* and *RmgGR119* genes interact differently during fungal infection – *Rmg8* prevents lesion development, while *RmgGR119* reduces the number of lesions.

The search for the identification of blast-resistant wheat genotypes has been a constant in researches. Seventy genotypes, between wheat cultivars and lines, as well as wheat-related wild species, were characterized at the seedling stage regarding their reaction to the inoculation of 18 M. oryzae isolates (Cruz et al., 2010). Three groups were identified with leaf blast severity ranging from 9.15-24.02%, 18.92-36.25%, and 16.07-61.65%, highlighting the variability of wheat reaction to the pathogen. Twelve of the accessions were selected to be inoculated at the adult plant stage. The genotypes derived from synthetic wheats showed the lowest severity in both flag leaves and spikes (Cruz et al., 2010). From a collection of 64 synthetic wheats, more than 10% were resistant to wheat blast, and 34% were moderately resistant, with one of them presenting an even lower progress of the disease (Cazal-Martínez et al., 2019). In evaluations under field conditions. Bolivian cultivars were identified as highly resistant to the disease, both in flag leaves and spikes (Kohli et al., 2011). A variability in the reaction to blast was also observed by Coelho et al. (2016) and Dianese et al. (2021) when working with different groups of wheat genotypes in Brazil. The continuous characterization of germplasm collections is key to strengthen knowledge about the genetic control of the disease and to find novel sources of resistance genes. Germplasm characterization is particularly important in hotspot locations where the highest disease levels have been recorded (Cruz et al., 2019; Dianese et al., 2021).

In these studies, the differential reaction of wheat accessions to different isolates of the pathogen was the common characteristic identified. With the inoculation of wheat cultivars, several groups of pathogen virulence were differentiated, including 14 virulence groups in leaves and 8 virulence groups in spikes (Maciel et al., 2014).

Against blast, complete resistance is not considered durable since it is controlled by a single gene. If there is any mutation in the pathogen's virulence gene, it is no longer recognized by the plant, preventing the defense reaction (Vale et al., 2001). In rice, the resistance conferred by R genes is broken within two to three years (Wang & Valent, 2017). Therefore, partial resistance is an important source of durable and broad-spectrum resistance. Durable resistance remains effective during its widespread and prolonged occurrence in environments favorable to the pathogen or disease.

Annually, the Brazilian Wheat and Triticale Research Commission provides information shared by the breeders on wheat cultivars indicated for cultivation in the country. For the 2019 growing season, 119 cultivars were recommended for the different wheat-producing regions (Reunião..., 2018). For 81 (68%) of them, information regarding the reaction to blast disease is available (Reunião..., 2018). Their reaction is classified as: susceptible, moderately susceptible, moderately resistant, and resistant. Some cultivars show intermediate levels such as susceptible/ moderately susceptible, moderately susceptible/ susceptible. moderately susceptible/moderately resistant, moderately resistant/moderately susceptible, and moderately resistant/resistant.

Over the years, the percentage of cultivars with information on reaction to blast has increased, partly due to the expansion of wheat cultivation in nontraditional regions, where blast occurrence is frequent. Figure 7 shows the numerical data of cultivars whose reaction to blast was characterized since 2007, when the different regional research commissions merged (Reunião..., 2008). For simplification, the types of reaction were grouped into four classes: susceptible, encompassing susceptible and susceptible/moderately susceptible; moderately susceptible, including moderately susceptible, moderately susceptible/susceptible, and moderately susceptible/moderately resistant; moderately resistant, encompassing moderately resistant, moderately resistant/moderately susceptible, and moderately resistant/resistant; and resistant. In 2007, information regarding reaction to wheat blast was available for only 37% of the cultivars, while in 2019, this percentage increased to 69%. The number of susceptible cultivars remained unchanged, whereas there was an increase in the number of wheat cultivars with some level of resistance. In 2019, 36 cultivars were classified as moderately resistant and 1 as resistant. For these cultivars, information about breeder company, year of release, pedigree, blast reaction, and the states/ regions indicated for wheat cultivation (Tables 1 and 2) are presented. Notably, 7 cultivars - BR 18 (Terena), CD 108, CD 116, CD 117, CD 118, IPR 85, and BRS Pardela – have been recommended for cultivation for at least ten years. BR 18 (Terena) has been endorsed for cultivation since its release in 1986 and is the only cultivar considered resistant to the disease (Reunião..., 2018). This makes it the oldest wheat cultivar with a durable resistance to blast in the country, being present in the pedigree of several wheat cultivars, including IPR 85 (moderately resistant) and BRS Pardela (moderately resistant/moderately susceptible); however, the pedigree of BR 18 is still unknown.

In 2011, wheat accessions with cultivar Milan in their pedigree were reported as presenting lower levels of blast in regions where the disease is endemic (Kohli



Figure 7. Frequency of classes of blast reaction of wheat (*Triticum aestivum*) cultivars recommended for cultivation in Brazil between 2007 and 2019. Data expressed as percentage. S, susceptible; MS, moderately susceptible; MR, moderately resistant; and R, resistant. Source: Reunião... (2018).

Cultivar	Company ⁽¹⁾	Year of release	Pedigree	Blast reaction ⁽²⁾
BR 18 (Terena)	Embrapa	1986	Unknown	R
BRS Graúna	Embrapa	2014	LD 975/WT 01121	MR/R
TBIO Audaz	Biotrigo	2017	TBIO Toruk/Celebra	MR/R
TBIO Mestre	Biotrigo	2012	IBIO 00810/Cronox//ORL 00255	MR/R
TBIO Sonic	Biotrigo	2017	TBIO Toruk/Celebra	MR/R
TBIO Sossego	Biotrigo	2015	BIO 08400 'S'/Quartzo//Quartzo	MR/R
BRS Gaivota(3)	Embrapa	2011	PF 940301/PF 940395	MR
CD 108	Coodetec	2003	TAM 200/Turaco	MR
CD 1104	Coodetec/Dupont	2014	CD 108/BRS 220	MR
CD 116	Coodetec	2006	Milan/Munia	MR
CD 117	Coodetec	2007	PF 87373/3/NS 713/PCI Sib // HAHN Sib	MR
CD 118	Coodetec	2008	Veery/Koel//Siren/3/Arivechi M 92	MR
CD 123	Coodetec	2010	BRS 177/CD 108	MR
CD 124	Coodetec	2012	ORL 95282 // IOC 8815/BR 35	MR
CD 1252	Coodetec/Dupont	2012	IPR 85/ORL 95282	MR
CD 1303	Coodetec/Dupont	2016	CD 150/BRS 177	MR
CD 1440	Coodetec/Dupont	2013	Ônix/CDFAPA 2001129	MR
CD 150	Coodetec/Dupont	2009	CD 104/CD 108	MR
CD 151	Coodetec/Dupont	2012	BRS 120/ORL 95282	MR
CD 1550	Coodetec/Dupont	2012	Ônix/CDFAPA 2001129	MR
CD 1805	Coodetec	2014	CDF 2040/Rubi	MR
Celebra	Biotrigo	2014	Marfim/Quartzo//Marfim	MR
FPS Amplitude	Biotrigo	2017	BIO 08407 Sib/Mirante	MR
IAC 381-Kuara	IAC	2009	CMH75.A.66/SERI/3/BH 1146//AA"S"WIN"S"	MR
IPR 144	IAPAR	2009	Seri*3/BUC/5/BOW/3/CAR 853/COC//Vee/4/OC22	MR
IPR 85	IAPAR	1999	Iapar 30/BR 18	MR
ORS 1401	OR	2015	Abalone//ORL 99075/Ônix	MR
ORS 1403	OR	2016	Inia Tijereta/Alcover//Abalone	MR
RBO 302	Tamona	2013	CB4a Ta 439 A/BR 18	MR
RBO 303	Tamona	2013	O8b2 Ta 439 A/Manitoba 96	MR
RBO 403	Tamona	2013	B3c1 IDS 762 U3c/BR 42	MR
TBIO Duque	Biotrigo	2017	Toruk#3/Celebra//Noble	MR
TBIO Ponteiro	Biotrigo	2017	Fuste/TBIO Mestre	MR
TBIO Sintonia	Biotrigo	2013	Marfim/Quartzo//Marfim	MR
BRS Pardela	Embrapa	2007	Trigo BR 18/PF 9099	MR/MS
FPS Virtude	Biotrigo	2015	ORL 04023/ORL 05003//CD 114	MR/MS
TBIO Energia I	Biotrigo	2016	IBIO 223/ORL 05690	MR/MS

Table 1. Wheat (*Triticum aestivum*) cultivars moderately resistant or resistant to wheat blast recommended for cultivation in Brazil in 2019.

⁽¹⁾Embrapa, Empresa Brasileira de Pesquisa Agropecuária; Biotrigo, Biotrigo Genética Ltda.; Coodetec, Coodetec Desenvolvimento, Produção e Comercialização Agrícola Ltda.; Dupont, Dupont do Brasil S/A – Divisão Pioneer Sementes; IAC, Instituto Agronômico; IAPAR, Instituto Agronômico do Paraná; OR, OR Melhoramento de Sementes Ltda.; and Tamona, Tamona Agropecuária Ltda. ⁽²⁾R, resistant; MR, moderately resistant; and MS, moderately susceptible. ⁽³⁾Previously named as BRS Albatroz. Source: Sousa & Caierão (2014) and Reunião... (2018).



Table 2. Brazilian states and homogeneous regions of adaptation for the cultivation of wheat (*Triticum aestivum*) cultivars moderately resistant or resistant to blast.

⁽¹⁾R, resistant; MR, moderately resistant; and MS, moderately susceptible. ⁽²⁾RHACT, homogeneous regions of adaptation of wheat cultivars. ⁽³⁾Brazilian states and federal district: PR, Paraná; RS, Rio Grande do Sul; SC, Santa Catarina; SP, São Paulo; MS, Mato Grosso do Sul; BA, Bahia; DF, Distrito Federal; GO, Goiás; MG, Minas Gerais; and MT, Mato Grosso. ⁽⁴⁾R, rainfed wheat; and I, irrigated wheat. ⁽⁵⁾Previously named as BRS Albatroz.Source: Reunião... (2018) and Brasil (2020).

et al., 2011). This is the case of cultivars Sausal CIAT, CD 116, and Caninde#1, released in Bolivia, Brazil, and Paraguay, respectively. The Milan cultivar has the 2NS/2AS translocation and was widely used in the wheat breeding program of Centro Internacional de Mejoramiento de Maíz y Trigo (CIMMYT). Phenotyping studies were conducted under controlled environmental conditions and under field conditions in Bolivia, aiming to evaluate the effect of 2NS translocation on blast resistance in winter and spring wheat cultivars (Cruz et al., 2016a). An association between the presence of 2NS translocation and wheat resistance to blast was found (Cruz et al., 2016a). Under controlled environmental conditions, the severity of spike blast in accessions with translocation (19.7%) was significantly lower than that in accessions without translocation (39.7% for winter wheats and 71.1% for spring wheats). However, the presence of 2NS does not confer leaf resistance to blast (Cruz et al., 2016a). In South America and Bangladesh, where the disease was recently identified, wheat accessions carrying 2NS translocation are currently being used for the introgression of translocation into elite lines (Cruppe et al., 2020).

Studies have also reported susceptible genotypes to *M. oryzae* even with the 2NS/2AS translocation (Cruz et al., 2016a; Ferreira et al., 2018; Cardozo Téllez et al., 2019), indicating the need to identify new sources of resistance. From 194 accessions without the 2NS/2AS segment and evaluated under field conditions, only four spring wheat from CIMMYT were identified as resistant or moderately resistant to wheat blast (Cruppe et al., 2020).

The use of a single source of resistance to *M. oryzae Triticum* in wheat breeding programs, therefore, jeopardizes its effectiveness due to the genetic variability of the pathogen. In most of the genetic backgrounds evaluated, the reduction in the severity of the disease in accessions with 2NS was lower when newer *M. oryzae* isolates were used in inoculations (Cruz et al., 2016a). This shows how the search for additional sources of resistance is essential. From nine Brazilian wheat accessions identified as resistant under field conditions, only the CPAC 07434 wheat line presented the 2NS/2AS translocation (Ferreira et al., 2018). Both the BR 18 (Terena) and BRS 229 cultivars, indicated for cultivation in regions where wheat blast frequently occurs, do not have the 2NS/2AS segment (Ferreira et al., 2018). These results are indicative of the potential of Brazilian germplasm as a valuable source of resistance genes to wheat blast.

Biotechnological strategies applied to wheat resistance

Up to date, molecular markers associated to wheat blast resistance *Rmg* genes have not been developed. This is important since the development of molecular markers for already identified genes is key to assist breeding programs, reducing the time required to develop a new cultivar.

2NS/2AS The translocation from Aegilops ventricosa Tausch, which shows an association with significant reductions in head blast in wheat genotypes (Cruz et al., 2016a), has been identified by the VENTRIUP and LN2 markers developed by Helguera et al. (2003). In another study, QTL mapping with a recombinant inbred line population, developed from Caninde#1 and Alondra, aimed to identify the QTL responsible for the 2NS/2AS translocation resistance to wheat blast disease (He et al., 2020); Caninde#1, the resistant parent, is a Paraguayan genotype and carries the 2NS/2AS translocation. A major QTL was found in the distal region of chromosome 2AS, explaining the range of phenotypic variation from 22.4 to 50.1%. The VENTRIUP/LN2 marker is at 0.0 cM, while the mapped QTL is 3.6 cM away from it (He et al., 2020). These findings indicate that new markers for the 2NS/2AS region could be an alternative to track resistance to wheat blast. Additional QTL with minor effects were identified on chromosomes 1AS, 2BL, 3AL, 4BS, 4DL, and 7BS (He et al., 2020).

Mapping populations with Brazilian germplasm have also been developed. A doubled-haploid population named Embrapa-Brusone, for example, was developed for genetic studies on resistance to blast (Ferreira et al., 2021). The parents of this population are: BRS 209, a wheat cultivar developed by Embrapa Soja and Embrapa Trigo (Sousa & Caierão, 2014) that is susceptible to the disease; and CBFusarium ENT014, a genotype from CIMMYT, which is resistant and carries the 2NS/2AS translocation. At the John Innes Centre, two biparental populations were developed using the single seed descent method. The BR 18 (Terena) Brazilian cultivar, resistant to wheat blast, was used as a common parent, while Anahuac 75 (susceptible) and BRS 179 (moderately resistant/susceptible) were the other parents in the cross (Goddard et al., 2020). The three abovementioned populations were used to identify QTL associated with wheat blast resistance. Besides the major effect of the 2NS/2AS region, QTL for ipr, explaining 11.8% of phenotypic variation, were identified on chromosomes 5B and 7B using the population obtained from cultivar BRS 209 and genotype CBFusarium ENT014 (Ferreira et al., 2021). In the study of two populations with BR 18, five QTL related to seedling resistance were located on 2B, 4B (two QTL), 5A, and 6A, whereas four QTL associated with spike resistance were located on 1A, 2B, 4A, and 5A. The phenotypic variation explained by these QTL varied from 5.9 to 24.8% (Goddard et al., 2020).

Genome-wide association mapping studies were carried out to identify chromosomal regions related to wheat blast disease. In a study with 271 lines from CIMMYT, chromosomal regions at 2AS and 3BL associated with wheat blast resistance were identified (Juliana et al., 2019). In a similar work, a region mapped on 2AS was also identified (Cruppe et al., 2021). In both researches, regions on the 2AS chromosome were associated with the 2NS translocation. The existence of other genomic regions besides the 2NS translocation associated with blast resistance reinforces the need for more genetic studies to validate the results already obtained and to identify new genes/sources of resistance.

Transcriptomic studies seeking to identify and understand molecular mechanisms associated with phenotypic differences among plant genotypes under pathogen infection can help explain the genetic basis of resistance. Seedlings of a wheat resistant cultivar, inoculated with adapted and nonadapted isolates of Magnaporthe, showed considerable reprogramming of the transcriptome (Tufan et al., 2009). A stronger induction of defense-related transcripts occurred at later times after infection, specifically from 24 hours post-inoculation onward, which was caused by adapted isolates of Magnaporthe in wheat leaves (Tufan et al., 2009). The calcium-mediated upregulation of defenserelated genes contributes to enhancing wheat resistance to blast fungus (Debona et al., 2017). Other authors found that chitinases also contribute to increasing wheat resistance to leaf blast (Xavier Filha et al., 2011). However, as stated before, the most serious blast disease damage occurs in wheat spikes. One of the rare reports about the differential reaction of wheat spikes compared responses to the inoculation of *M. oryzae* and *Fusarium graminearum* (Ha et al., 2016), which is the causal agent of Fusarium head blight, another severe disease of wheat spikes. Differential responses of wheat to both pathogens were observed, and three genes were particularly upregulated after *M. oryzae* inoculation: a chitinase (*Chi2*) and two thaumatin-like proteins (*PR2* and *PR5*) (Ha et al., 2016).

Studies based on transcriptome profiling using RNA-sequencing allow to broadly identify changes in gene regulation. Seeking to better understand the molecular basis of interactions between wheat and MoT, the parents of the Embrapa-Brusone population used in QTL studies were also analyzed with RNAsequencing (Ferreira et al., 2020). When comparing spikes that are mock or inoculated with MoT, transcriptome changes were detected between cultivar BRS 209, which is highly susceptible, and genotype CBFusarium ENT014, which is resistant to bleaching development. After pathogen infection, 388 and 249 differentially expressed genes (DEGs) in cultivar BRS 209 and in genotype CBFusarium ENT014 were found, respectively (Figure 8). This result is quite interesting, as the susceptible reaction showed a larger number of DEGs than the resistant one. For rice blast,



Figure 8. Venn diagram of differentially expressed genes found in the RNA-sequencing experiment with spikes of the BRS 209 cultivar and CBFusarium ENT014 genotype of wheat (*Triticum aestivum*) subjected or not to inoculation with *Magnaporthe oryzae Triticum*. The RNA-sequencing data were tested using a maximum false discovery rate of 0.001.

more drastic changes in gene expression are observed in incompatible rather than in compatible interactions (Kawahara et al., 2012). From the 249 DEGs identified in the blast-resistant wheat genotype, 23 up- and 1 down-regulated were annotated as related to defense responses (Figure 9) (Ferreira et al., 2020).

Future studies should consider the DEG related to defense responses to spike blast infection and the identification of wheat QTL for the population doubled-haploid lines from cultivar BRS 209 x genotype CBFusarium ENT014. The genetic regulation of flowering time in rapeseed (*Brassica napus* L.), for example, was investigated adopting a similar approach (Jian et al., 2019), in which 45 flowering time-related genes were identified in the 27 detected QTL. Therefore, DEGs can be used to explain the identified QTL and to develop new molecular markers. Another possibility to explore transcriptomic data is to search for single nucleotide polymorphisms (SNPs) between the mRNA sequences



Figure 9. Heatmap showing the differential expression of defense-related genes in wheat (*Triticum aestivum*) genotypes (CBFusarium ENT014 and cultivar BRS 209) under control conditions (C) or inoculated (I) with *Magnaporthe oryzae Triticum*. Relative expression levels are displayed as log2 centered averages of normalized expression values from three biological replicates. Transcript sequences are designated by "TRINITY...", followed by the probable gene name and protein name according to SwissProt (2021), i.e.: MIK2, MDIS1-interacting receptor-like kinase 2/probable leucine-rich repeat receptor-like protein kinase; Y2241, putative leucine-rich repeat receptor-like serine/threonine-protein kinase; Y3475, probable LRR receptor-like serine/threonine-protein kinase; LRL26, protein suppressor of NPR1-1 constitutive 4; CHIA, basic endochitinase A; WIR1A, protein WIR1A; TLP, thaumatin-like protein PWIR2; PR1C, pathogenesis-related protein IC; BAK1, LRR receptor kinase SERK2; E13B, glucan endo-1,3-beta-glucosidase GII; Y2913, G-type lectin S-receptor-like serine/threonine-protein kinase; CRK5, probable LRR receptor-like serine/threonine-protein kinase 5; CRK25, cysteine-rich receptor-like protein kinase 6; PER1, peroxidase; SD11, G-type lectin S-receptor-like serine/threonine-protein kinase 5], Protein kinase SD1-1; Y5188, probable LRR receptor-like serine/threonine-protein kinase 3.

of the resistant and susceptible wheat genotypes. In addition, the functional annotation of SNPs can disclose their importance for wheat blast resistance. The developed markers can be used, in the future, for developing wheat blast-resistant cultivars.

Concluding remarks

In Brazil, wheat blast is a current constraint to wheat cultivation in tropical areas from the Cerrado and Mata Atlântica biomes and in the subtropical region of the state of Paraná, where it is endemic and outbreaks are frequent. Managing these regions is essential for Brazilian wheat production to reach self-sufficiency. It is important to emphasize that all management strategies aiming to control blast disease must be combined to reduce yield losses, especially with the choice of wheat cultivars with moderate resistance. Several cultivars with some resistance to blast are currently available for cultivation in the country, including those that are non-2NS carriers. Furthermore, the genetic control of wheat blast will be even more efficient with the continuous search for new sources of resistance and the use of molecular markers. whose development is already underway.

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